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Seasonal Patterns of Fecundity and Diet of Roof Rats in a Hawaiian Macadamia Orchard

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Abstract

We determined seasonal patterns of fecundity and diet of roof rats (*Rattus rattus*) snap-trapped in an orchard of macadamias (*Macadamia integrifolia*), and assessed the implications for controlling rat damage to macadamia nuts. In all, 903 males, 756 females, and 16 rats of unidentified sex were captured between June 1990 and April 1991. Sex ratios varied from 1 : 1 only during August, when males outnumbered females ($P < 0 \cdot 05$). Subadult rats were present throughout the study and comprised 31% of captures. Adult male roof rats were in reproductive condition throughout the year, and females bore young during every month of the study. Average monthly pregnancy rates varied from 8% to 54% and were highest in April. Mean prenatal litter size ranged from 3·0 to 6·5 among months. Macadamia nut was the dominant food item throughout the study, and was present in all 199 stomachs inspected, with a mean relative frequency of 85%. Insect fragments, primarily lepidopteran larvae, occurred in 66% of the stomachs, with a mean relative frequency of 8%. Moss was found in 48% of the stomachs, with a mean relative frequency of 4%. Grass seeds, fruit seeds and non-insect animal material were present in small amounts. These results show that, in areas with prolonged macadamia flowering and subsequent extended periods of nut availability, roof rats breed throughout the year on a diet consisting mostly of macadamia nuts. In such situations, growers may need to apply control measures throughout the crop cycle to keep rat damage at acceptable levels.

Introduction

A better understanding of the biology of rodent pests in specific cropping systems can lead to improved strategies for reducing damage. For example, knowledge of food preferences and seasonal variations in diet indicates which rodenticide baits are most likely to be eaten by the target organism, and may provide a basis for manipulating pest populations through habitat manipulation. California ground squirrels (*Spermophilus beecheyi*) eat grain baits during the dry season, when they gather and pouch seeds, but not during the rainy season, when they feed primarily on green vegetation (Dana 1962; Salmon and Lickliter 1983). Artichoke farmers in California use artichoke bracts (*Cynara scolymus*) instead of grain as a rodenticide bait because voles (*Microtus californicus*) prefer the former to other foods available in artichoke fields (Marsh and Tunberg 1985; Koehler *et al.* 1989). Australian sugarcane growers reduce damage by *Rattus sordidus* by eliminating in-crop weeds necessary for breeding (Whisson 1993).

Knowledge of seasonal reproductive patterns can be used to predict population densities and subsequent crop susceptibility to damage; these patterns can also indicate the most effective times to apply control measures. Cantrill (1992) developed an early-warning system for predicting irruptions of house mice (*Mus domesticus*) in Australian grain crops,

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which warned up to nine months in advance on the basis of population densities at the start of the breeding season. Marsh and Tunberg (1985) found that most rodent damage in Californian artichoke fields coincided with breeding activity of voles, and thus recommended applying control measures before or at the start of the autumn breeding season.

Roof rats (*Rattus rattus*) cause extensive damage in Hawaiian macadamia orchards (Fellows *et al.* 1978; Pank *et al.* 1978; Tobin *et al.* 1993). However, little is known about the ecology of rats in macadamia orchards. A better understanding of the diet and life-history characteristics of rats in this type of habitat could lead to the development of more-effective and more-selective control strategies. Therefore, we examined seasonal variations in the diet and fecundity of roof rats captured in a Hawaiian macadamia orchard.

Methods

Study Area

This study was conducted at the Mauna Loa Macadamia Nut Corporation macadamia orchard in Keaau, about 17 km south of Hilo, Hawaii. This orchard comprised 999 ha and was divided into blocks of 10–30 ha separated by dirt roads and windbreaks of Norfolk Island pine trees (*Araucaria heterophylla*). Rats were trapped in portions of four blocks ranging in size from 8·0 to 10·6 ha and containing mostly 20-year-old macadamia trees; 17–23% were replanted trees that had replaced wind-damaged, diseased or dead trees. One block was surrounded by other macadamia blocks, two were bordered on one side by a fallow area vegetated with various introduced plants, and the fourth abutted an overgrown, abandoned orchard on one side and a paved road on the opposite side. The ground throughout the orchard consisted of porous lava rock overlain with 8–15 cm of soil and sparse, irregularly distributed weeds.

The blocks each contained several varieties of macadamia trees that flowered asynchronously, with individual varieties flowering over a period of several months. Thus, macadamia nuts were available in the orchard throughout the year. Mature nuts dropped from the trees and were harvested from the ground at intervals of 6–8 weeks. The nuts in the four blocks were harvested at different times.

Trapping

Rats were collected between June 1990 and April 1991 in conjunction with a study that evaluated snap-trapping as a method for controlling damage (Tobin *et al.* 1993). One to four weeks after each of four or five harvests in each block, we secured 41–49 unset rat snap traps (McGill Metal Products Company or Woodstream Corporation) per hectare to lower, lateral branches and prebaited them with chunks of fresh coconut. Three or four days later we rebaited the traps with fresh coconut and set them. Rat carcasses were collected daily, placed in plastic bags, and refrigerated (or frozen if kept for longer than two days) at the Denver Wildlife Research Center field station in Hilo, Hawaii, until processed. Because the timing of each trapping session was determined by when each block was harvested, trapping effort varied among months (Table 1).

Age and Reproductive Condition

Frozen carcasses were thawed before they were inspected for age and reproductive condition. We recorded sex, body weight, perforate or imperforate vagina, enlarged or lactating nipples, and scrotal or non-scrotal testes. Males with scrotal testes, females with perforate vaginas, and rats weighing at least 90 g were classified as adults (Hirata and Nass 1974). We made a midline incision along the ventral surface of each rat and recorded the number of macroscopically visible embryos and foetuses, and the presence or absence of uterine scars. Resorbing embryos were noted, but were not included in counts of prenatal litter size. On the basis of embryo or foetal development, we classified each pregnancy as very early (just detectable through the uterine wall), early (embryos spherically shaped, features indistinguishable), midterm (foetuses moderate-sized, shape no longer spherical, features becoming discernable), or near term (foetuses approaching birth size, features well defined). We evaluated whether the sex ratio differed from 1 : 1 during each month with a chi-square test for goodness of fit (Sokal and Rohlf 1981). We used a chi-square test to evaluate whether the rate of pregnancy varied among months, and ANOVA and Bonferroni's t-test to compare litter sizes among months (SAS Institute 1988).

Table 1. Monthly trapping effort in each of four blocks in a Hawaiian macadamia orchard

The four blocks were harvested asynchronously, and trapping was scheduled relative to when each block was harvested; 41–49 traps ha^{-1} were set and monitored for eight nights after each of four or five harvests in each block

Month	Trap-nights Block 2 (10·5 ha)	Block 5 (8·0 ha)	Block 7 (10·6 ha)	Block 19 (8·7 ha)	Total
Jun. 1990	3736	0	0	0	3736
Jul. 1990	0	1960	433	0	2393
Aug. 1990	0	1176	2598	3280	7054
Sep. 1990	2802	3136	1732	0	7670
Oct. 1990	0	0	1732	2870	4602
Nov. 1990	3736	1568	0	0	5304
Dec. 1990	0	1568	3464	3280	8312
Jan. 1991	3736	3528	1299	0	8563
Feb. 1991	0	0	2165	3280	5445
Mar. 1991	3269	2744	0	0	6013
Apr. 1991	0	0	3464	3280	6744

Dietary Analysis

We removed stomachs, together with 0·5–1·0 cm of the oesophagus and intestine, from rats, placed them individually in labelled plastic freezer bags, and froze them at −10°C. Ten stomachs of adult rats per block per trapping session were systematically selected from a list and examined (only nine stomachs were available that met our examination criteria from the final session in one block). We removed each stomach from its plastic bag and, without allowing it to thaw, made an incision along the entire length of the convex surface, peeled back the stomach wall, and rinsed the contents into a 100-mL beaker with a 2% detergent solution. Approximately 50 mL of the detergent solution were then added and swirled for 5 min to separate the contents and dissolve gastric juices, stomach oils, and grease. The contents of the beaker were poured into a 35-mesh (0·5-mm opening) sieve and rinsed with tap water until the filtrate appeared clear. We removed parasitic roundworms and replaced 13 stomachs that contained more than 50% by volume roundworms.

We removed excess water by dabbing the bottom of the sieve with a paper towel, and recorded the wet weight of the processed stomach contents. A 0·62-mL sample of the contents was mixed with 10 mL of tap water in a Petri dish; 41 stomachs containing less than 0·62 mL were replaced.

The Petri dish was placed inside an inverted Petri-dish cover lined with a grid of 7-mm^2 squares. We examined 40 preselected squares at 8–10× magnification under a dissecting microscope and recorded the food types present in each. When necessary, a higher magnification (15–30×) was used to identify items. Seven samples with more than trace amounts of coconut (the bait used in the traps) were replaced. We calculated the relative frequency as

$$\frac{\text{(number of squares in which a food item occurred)}}{\Sigma\text{(number of squares occupied by individual food items)}} \times 100 .$$

Reference to commercial products for identification does not imply endorsement by the authors or the U.S. Department of Agriculture.

Results

Captures

We captured 1675 roof rats between June 1990 and April 1991, including 903 males (70% adult), 756 females (69% adult), and 16 partially eaten rats (6% adult) the sex of which we could not determine. Capture success was low in June, increased in July, and declined steadily each month thereafter (Fig. 1). The only month during which the sex ratio varied from 1 : 1 was August ($\chi^2 = 4 \cdot 37$, $P < 0 \cdot 05$), when we captured more males that females, particularly among adults ($\chi^2 = 8 \cdot 10$, $P < 0 \cdot 005$) (Fig. 1). Subadult rats were present in the orchard throughout the study and comprised 31% of all captures, ranging from 23% in December to 46% in June (Fig. 1).

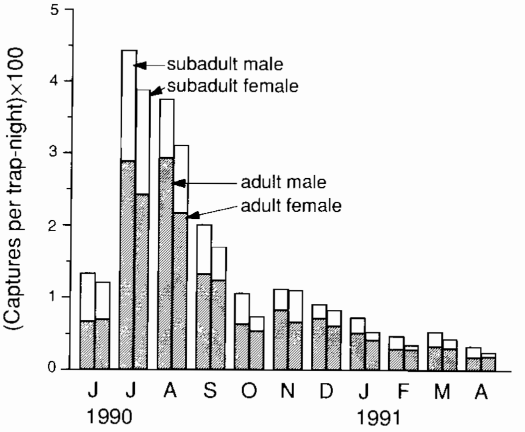

Fig. 1. Number, sex and age of roof rats (*Rattus rattus*) captured in a Hawaiian macadamia orchard, June 1990 to April 1991.

Reproductive Characteristics

The proportion of adult females that were visibly pregnant varied among months ($P = 0 \cdot 017$) and ranged from a low of 8% in June 1990 to a high of 54% in April 1991 (Table 2). These values probably underestimate the actual rate of pregnancy, as they do not include pregnant animals whose embryos had not implanted or were too small to be detected through the uterine wall. In all, 12–33% of adult female roof rats had uterine scars indicating previous pregnancies (Table 2).

Prenatal litter size was similar among most months; however, fewer embryos were detected per female in December and January than in June ($F_{10,98} = 1 \cdot 90$, $P = 0 \cdot 05$) (Table 2). Our embryo counts probably overestimate litter sizes at birth because of prenatal mortality, which varies depending on the stage of gestation (Loeb and Schwab

Table 2. Percentage of adult females that were pregnant, lactating or had uterine scars, and mean litter size of roof rats (*Rattus rattus*) captured in a Hawaiian macadamia orchard, June 1990 to April 1991

Pre-birth litter sizes varied depending on the stage of gestation and tend to overestimate litter sizes at birth

Month	*n*	Pregnant (%)	Mean litter size (s.e.)	Lactating (%)	Scars (%)
Jun. 1990	26	8	6·5 (0·5)	0	31
Jul. 1990	58	12	4·1 (0·5)	0	12
Aug. 1990	150	22	3·9 (0·2)	7	33
Sep. 1990	95	26	3·9 (0·3)	16	29
Oct. 1990	24	29	3·9 (0·3)	4	29
Nov. 1990	35	9	3·0 (0·6)	9	23
Dec. 1990	51	16	3·1 (0·6)	6	20
Jan. 1991	36	22	3·3 (0·2)	0	22
Feb. 1991	15	27	3·3 (0·3)	0	27
Mar. 1991	18	28	4·2 (0·4)	6	28
Apr. 1991	13	54	4·0 (0·6)	8	15

1987). Of the 109 litters in this study, we observed resorbing foetuses in only six midterm litters and two near-term litters. Five litters had one foetus, two had two, and one had three foetuses being resorbed. Lactating females were captured in the orchard during all months except June, July, January and February, and were most prevalent in September (Table 2).

We did not examine cauda epididymis tubules or evaluate sperm production, but external sexual characteristics indicated that the male roof rats in our study remained in a reproductive state throughout the year. The four non-scrotal males that we classified as adults on the basis of their weight were probably young males that were not yet fecund.

Table 3. Percentage occurrence and relative frequency (in parentheses) of dietary items identified in stomachs of roof rats (*Rattus rattus*) captured in a Hawaiian macadamia orchard, June 1990 to April 1991

Percentage occurrence is the percentage of stomachs in which food item occurred. Relative frequency (RF) of food items in each stomach was determined with a sampling grid of 40 squares; RF = [(number of squares in which a food item occurred)/Σ(number of squares occupied by individual food items)]$\times$100

Month	No. of rats	Macadamia nuts	Insect	Moss	Other vegetation	Seeds	Non-insect animal
Jun. 1990	10	100	70	70	0	0	10
		(91)	(4)	(5)	(0)	(0)	(<1)
Jul. 1990	10	100	40	60	20	0	10
		(90)	(3)	(6)	(<1)	(0)	(<1)
Aug. 1990	20	100	70	50	5	10	0
		(85)	(7)	(6)	(<1)	(2)	(0)
Sep. 1990	29	100	69	35	10	0	7
		(90)	(8)	(1)	(<1)	(0)	(<1)
Oct. 1990	11	100	64	46	0	0	0
		(93)	(4)	(3)	(0)	(0)	(0)
Nov. 1990	16	100	75	38	6	6	6
		(85)	(9)	(3)	(<1)	(2)	(1)
Dec. 1990	24	100	67	54	17	0	0
		(83)	(8)	(6)	(3)	(0)	(0)
Jan. 1991	25	100	60	32	16	4	0
		(89)	(6)	(2)	(2)	(1)	(0)
Feb. 1991	15	100	87	67	0	0	0
		(69)	(25)	(7)	(0)	(0)	(0)
Mar. 1991	20	100	60	15	0	20	0
		(78)	(11)	(2)	(0)	(9)	(0)
Apr. 1991	19	100	63	63	5	0	5
		(83)	(8)	(8)	(<1)	(0)	(2)
Mean		100	66	48	7	4	3
		(85)	(8)	(4)	(<1)	(1)	(<1)

Diet

Macadamia nuts were the major item in all 199 stomachs examined (Table 3). Fragments of macadamia nuts were present in stomach samples with an average relative frequency of 85%. Insect fragments were found in 66% of the stomachs and had a relative frequency of 8%. Lepidopteran larvae were identified in 26% of the stomachs and occurred in samples with a relative frequency of 6%. The most common larva was the moth *Elydna nonagrica* (Noctuidae). Moss sporophytes, seta or capsules were present in almost half of the stomachs and had a relative frequency of 4%. *Sematophyllum saespitosum* comprised more than 95% of the mosses. In all, 5% of the stomachs contained broadleaf vegetation, 1% contained roots, and 3% contained unidentified vegetative material. Non-moss vegetation occurred with a relative frequency of <1%. Fruit seeds occurred in 4% of the stomachs with a relative frequency of 1%. A total of 2% of the stomachs had fragments of feathers, 2% contained fragments of mollusc shells, and 1% had flesh. These non-insect animal materials occurred with a relative frequency of less than 1%.

Discussion

Captures and Reproductive Characteristics

The 1675 roof rats we examined were collected as part of a study to evaluate snap-trapping as a method for reducing rat damage to macadamia nuts, and the trapping schedule designed for this purpose resulted in unequal trapping effort among months. The low initial capture success in June may be due to the fact that only one block was trapped during this month, and it had lower capture success than the other blocks during most of the study. The steady decline in monthly capture success after July probably reflects a decline in populations, because traps were repeatedly set in the same blocks. The similar capture success of males and females has been observed in other Pacific island populations of roof rats (Ponape, Jackson 1962*a*; Oahu, Tamarin and Malecha 1971, 1972; New Zealand, Best 1973). Subadult rats were present throughout the study.

Pregnancy rates and litter size were comparable to those reported for roof rats in other areas (pregnancy—Davis 1953; Jackson 1962*b*; Best 1973; litter size—Davis 1953; Jackson 1962*b*; Daniel 1972; Tamarin and Malecha 1972; Best 1973). Like Jackson (1962*b*) and Loeb and Schwab (1987), we observed resorbing foetuses only in the later stages of pregnancy. Similar to roof rats captured in a forest area on Oahu (Tamarin and Malecha 1971), the percentage of adult females that were lactating peaked during the autumn, declined to zero during most of the winter, and varied during spring and summer. That we captured few lactating females during any month suggests that nursing females restrict their movements and are less susceptible to capture. Similar to roof rats in other areas (Jackson 1962*b*; Daniel 1972; Best 1973), adult males remained in reproductive condition throughout the year.

Many rodent species are opportunistic breeders, with males remaining capable of breeding throughout the year, and females breeding continuously or seasonally depending primarily on energetic and nutritional considerations (Bronson and Perrigo 1987). Different populations of roof rats have shown unimodal, bimodal, irregular and continuous patterns of reproduction (Davis 1953; Jackson 1962*b*; Tamarin and Malecha 1971, 1972; Daniel 1972; Best 1973). Roof rats captured in sugarcane fields and forested areas near our study site had their highest level of reproduction in late summer to mid-autumn, with a peak in August, and little or no reproduction from December to February (Fellows and Tsutsui 1977). The rats in the macadamia orchard where we conducted our study bred throughout the year.

Diet

Macadamia nuts were the major item in all stomachs examined, with small amounts of insect matter, particularly lepidopteran larvae, found in two-thirds of the stomachs. Except for dead and dying leaves and dropped macadamia nuts that accumulated between harvests, the orchard floor was largely barren. Grasses, other ground vegetation, and non-macadamia foods were scarce. The small quantity of insects found in more than half of the rat stomachs probably provided protein. Macadamia nuts are rich in high energy fatty acids, but contain limited amounts of amino acids (Cavaletto 1980). Fellows and Sugihara (1977) suggested that rats in sugarcane fields subsist primarily on sugarcane but consume small amounts of arthropods for protein. The mosses found in this study were probably ingested incidently. *Sematophyllum saespitosum* is ubiquitous throughout low-elevation disturbed areas in Hawaii and in this study it was common on branches, tree trunks and husks of macadamia nuts.

Management Implications

The presence of energy-rich, nutritious food in large part determines when breeding occurs in muroid rodents (Bronson and Perrigo 1987). In Malaysia, rice rats (*R. argentiventer*) displayed a unimodal breeding pattern in single-cropped fields and a bimodal breeding pattern in double-cropped fields, with reproduction corresponding with the reproductive and ripening phases of the rice crop (Lam 1983). On the island of Hawaii, roof rats reproduced throughout the year in macadamia orchards (this study), but only seasonally in nearby sugarcane fields and forests (Fellows and Tsutsui 1977).

Macadamia orchards in Hawaii provide an ideal habitat where rats live and reproduce year-round. The thick canopy and interlocking branches of mature trees provide nesting sites and facilitate the movement of rats among trees. The lava rock substratum forms natural cavities and crevices where rats can burrow and nest beneath the orchard floor away from predators and the disturbance of orchard operations. A prolonged flowering season results in an almost continuous availability of macadamia nuts, which enables rats to subsist and reproduce throughout the year. Breeding may be more seasonal in macadamia orchards with more condensed flowering and nut-development periods, such as in Australia (Vock 1989). In Hawaii, growers may have to apply control measures on a continuous basis to keep rat damage at acceptable levels.

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